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Insect visitation and pollen deposition in an invaded prairie plant community

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ABSTRACT

Invasive plants with large flowering displays have been shown to compete with native plants for pollinator services, often to the detriment of native plant fitness. In this study, we compare the pollinator communities and pollen deposited on stigmas of native plant species within and away from stands of the invasive alien plant, leafy spurge (*Euphorbia esula*) at a large natural area in North Dakota, USA. Specifically, we ask if infestation influences (1) visitation rates and taxonomic composition of visitors to native flowers, and (2) the amount of conspecific pollen, number of pollen species, and proportion of heterospecific pollen on stigmas of native plants. We observed visits to selected native species during May and June 2000 and 2001. Stigmas were collected from a subsample of the flowers within these plots, squashed, and the pollen identified and counted under a light microscope. Visitation varied between years and among species of native plants: infestation had mixed effects in 2000 but visitation, especially by halictids was always lower within infestations in 2001. Despite differences in visitation between years, we found significantly less conspecific pollen on stigmas from infested plots in six of eight cases; we never found significantly more conspecific pollen on stigmas from within infestations. Our results emphasize the temporal variability in plant–pollinator relations and the added complexity imposed by an invasive species that will always make prediction of effects difficult. Nonetheless, the consistently lower conspecific pollen counts on native stigmas within infestations, regardless of visitation, suggest the likelihood of negative effects.

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1. Introduction

Many alien plants form dense monospecific stands that flower profusely, and thus may introduce substantial amounts of alien pollen and nectar into the native communities they invade. The diffuse nature of pollination mutualisms (Palmer et al., 2003) and the multiple interspecific interactions involved (Waser et al., 1996) make the outcome of such an influx of resources highly uncertain. If an increase in resources attracts a disproportionately larger number of pollinators to the area, pollination of native plants in the vicinity of the

infestation could be enhanced (Feldman et al., 2004); however, if those pollinators preferentially visit the invasive species, visitation to, and therefore pollination of, native plants could be depressed (Rathcke, 1983). Because pollination systems tend to be generalized, especially in the northern temperate zone of North America (Johnson and Steiner, 2000), pollination of native plants also could be depressed if pollinators that visit native plants deposit alien pollen on their stigmas, and much of the native pollen is carried to aliens, rather than to conspecifics (improper pollen transfer (IPT); Waser, 1978; Rathcke, 1983). Alien pollen that makes its way to native plant

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stigmas may affect reproduction by clogging or mechanically blocking the stigma or style, by chemically interfering with fertilization (allelopathy), or by producing hybrids (Brown and Mitchell, 2001; McLernon et al., 1996; Waser, 1978).

Indeed, evidence has begun to accumulate that suggests invasive plants with large flowering displays can compete with native plants for pollinator services, often to the detriment of native plant fitness. Effects have been documented in terms of both pollen quantity and quality (Brown and Mitchell, 2001; Brown et al., 2002; Chittka and Schürkens, 2001; Moragues and Traveset, 2005). What is not yet clear is whether the change in pollination success is due to the change in the prevalence of exotic pollen, which is dispersed (at the expense of native pollen) by the same generalist pollinator community that existed prior to infestation, a change in the pollinator community that visits native plants to fewer or less efficient pollinators, a change in rates of visitation to flowers, or some combination of these. If plants compete for pollinator services, a new plant species that provides copious resources will dramatically alter the competitive relationships within the plant community, with less abundant species being put at a distinct disadvantage (Palmer et al., 2003), especially with respect to constant pollinators that specialize on abundant and rewarding flowers (e.g., Gegear and Lavery, 1998, 2004; Kunin, 1993). In contrast, if pollinators compete for floral rewards, introduction of a super-abundant resource may mean that pollen and nectar are no longer limiting, and new or formerly out-competed insect taxa may enter the system. These issues are of concern not only with respect to potential effects on pollen-limited plants, but also in light of recent indications of declining pollinator populations (Kearns et al., 1998; Spira, 2001).

In this study, we compare the pollinator insect communities and pollen delivered to stigmas of native plant species within and >100 m away from stands of the invasive alien plant, leafy spurge (*Euphorbia esula* L.; Euphorbiaceae; hereafter *Euphorbia*). Specifically, we ask (1) does visitation to native flowers by pollinator insect taxa vary between infested and non-infested sites, (2) does the amount of conspecific pollen on stigmas vary between infested and non-infested sites, and (3) does infestation influence the number of pollen species and proportion of heterospecific pollen on native plant stigmas? If the presence of *Euphorbia* facilitates pollination of native species, we would expect more visitation and greater amounts of conspecific pollen on stigmas of native flowers in infested sites compared with non-infested sites. On the other hand, if *Euphorbia* competes with native species for pollinators, we would expect fewer visits and less conspecific pollen on native stigmas in infested sites. Less conspecific pollen on native stigmas could also result from a change in the pollinator community within infested sites to species that are less constant in visitation habit; if this is the case, we would expect to find a higher diversity of pollen species on stigmas in infested sites.

2. Methods

2.1. Study site

The study was conducted in the South Unit of Theodore Roosevelt National Park (TRNP) in western North Dakota, USA.

Vegetation at the park is dominated by native cool season grasses, primarily *Pascopyrum smithii* and *Stipa* spp. The south unit of the park was established in 1947 and contains free-ranging native ungulates as well as a small herd of wild horses. More detail on plant species associations within the park can be found in Larson et al. (2001). *E. esula* was first documented in the South Unit of TRNP in 1970 (unpublished park documents). Infested and non-infested areas used in this study had been so since at least 1996.

Euphorbia esula is a Eurasian perennial that invades mixed-grass prairie in rangeland and natural areas throughout the northern Great Plains and causes extensive environmental and economic damage (Bangsund et al., 1996, 1999; Trammell and Butler, 1995). Aerial photography in 1991 indicated approximately 1620 ha of *Euphorbia* in the South Unit of TRNP, with the distribution closely aligned with watercourses and drainages. *Euphorbia* flowers profusely during June in North Dakota, bearing terminal umbels with sequentially maturing female and male flowers (cyathia); each “wave” of flowers produces 5–12 female followed by 11–20 male flowers and each stem may branch to produce as many as 16 umbels (Selleck et al., 1962). Each plant's yellow flowers mature in succession over a period of several weeks. Pollen remains viable for up to 2 days on each flower and nectar is produced by the glands of the cyathium 3–8 days after inversion of the female flower (Selleck et al., 1962), so a consistent source of pollen and nectar remains available for approximately 6 weeks at our study sites. Capsules, which are explosively dehiscent, mature in mid- to late-summer and contain up to three seeds.

2.2. Sampling design

Using data from a 1996 stratified-random survey of plants in the South Unit in which >800 geo-referenced transects were examined (methods for the survey can be found in Larson et al. (2001)), we identified areas within the South Unit that were likely to have one of several concurrently blooming native plants, either >100 m away from or within a *Euphorbia* infestation. We avoided the dwarf sagebrush (*Artemisia cana*) and river bottom vegetation types because they harbor large populations of a variety of non-native species (Larson et al., 2001). All sampling was done in upland prairie to minimize bias in insect habitat characteristics that could be associated with infested versus non-infested habitats. For an area to be considered infested, it had to have flowering *Euphorbia* stems intermixed with flowering native species; total area of each infestation varied from tens of square meters to a hectare or more. In consideration of the necessary sample size, only relatively common species were selected as target native species. We narrowed our target native species to only those that, upon field inspection, occurred both within and at least 100 m away from an infestation and that bloomed concurrently with *Euphorbia*. While 100 m is admittedly arbitrary, it was the largest area we could reasonably search exhaustively for the presence of *Euphorbia*. Our goal was to minimize the chance that insects that had visited *Euphorbia* would arrive at our non-infested plots. Target native species in 2000 were *Campanula rotundifolia* L. (Campanulaceae) for visitation only and *Linum lewisii* Pursh var. *lewisii* (Linaceae) and *Oxytropis lambertii* Pursh var. *lambertii* (Fabaceae) for pollen counts and

visitation. In 2001 we added *Calylophus serrulatus* (Nutt.) Raven (Onagraceae), *Sphaeralcea coccinea* (Nutt.) Rydb. ssp. *coccinea* (Malvaceae), and *Vicia americana* Muhl. ex Willd. (Fabaceae) for pollen counts (we were unable to obtain a sufficient sample size to analyze visitation to these species), and conducted pollen counts on *Campanula*. Of these, *Linum*, *Campanula*, *Calylophus* and *Sphaeralcea* as well as *Euphorbia* have actinomorphic (i.e., radially symmetrical) flowers, although *Campanula* is bell-shaped and must be entered from below, and *Oxytropis* and *Vicia* have zygomorphic (i.e., bilaterally symmetrical). Taxonomy follows the USDA Plants data base (USDA 2004). We use the genus name to refer to these species throughout the paper.

2.3. Visitation

We assessed visitation to native flowers and to those of *Euphorbia* within 1 m² square plots that contained at least six (total) individual flowering stems of one or more of the native target species. Plots were located in the vicinity of one of the survey transects (described above) where a target species occurred and were positioned so that the required number of target species was included in the plot. We counted the number of flowers of each target species, *Euphorbia* inflorescences, and any other species in flower within the plot. In addition, we counted the number of flowers by species in six 0.25 × 0.25 m quadrats in each of the four cardinal compass directions outside the plot, since flower density may influence visitation and our plots might not adequately reflect density at the scale perceived by pollinators. Visitation on most plots was assessed once in the morning and once mid-day, weather permitting; results were averaged for each plot prior to analysis. Different plots were established each day.

Observations lasted 20 min, during which time each pollination event on each target flower was recorded on a data sheet. We defined a pollination event (hereafter termed “visit”) as any contact of an insect with anthers or stigmas on an individual flower. We recorded the flower species visited and the insect to the lowest field-identifiable taxonomic category (see below). At the end of the 20-min period, a new plot was established in a new location and the process repeated. Observations were made between 07:00 and 14:30 (most after 08:00) with temperatures between 14 and 35 °C. We did not conduct observations if winds were in excess of Beaufort 4 (5–6 knots) or if it was raining. We assessed insect visitation on 233 plots (77.67 h at 20 min/plot) over the two year period and recorded 763 individual insect visits in 2000 and 812 in 2001.

A haphazard sample of bees was collected at each area where visitation was assessed during the 2000 field season and sent to a taxonomic expert for identification. Observers were trained to identify common bee families prior to beginning work. They were often able to distinguish *Bombus*, *Apis*, *Halictus*, *Dialictus*, *Agapostemon* and *Lasioglossum*, but native bees could not be identified to species in the field. We did not distinguish among taxa of wasps because we could not reliably discern taxa in the field, or lepidopterans because visitation rates were low enough that individual taxa could not be analyzed statistically. Flies were overwhelmingly muscoid, and taxa were not separated for analysis.

2.4. Pollen loads on stigmas

Prior to beginning observations (described above), four flowers of the target species in each plot were chosen arbitrarily and marked with a small bit of pastel-colored thread, each a different color. The thread did not appear to influence pollinators; none investigated the thread and marked flowers were no more likely to be visited than unmarked flowers (data not shown). After observations were completed for that day, we collected stigmas of the four marked flowers in each plot and placed them individually in glassine envelopes. Upon returning to the lab, stigmas were placed on microscope slides with a drop of resin-based mounting medium. The cover slip was pressed firmly over the stigma to squash it and force the pollen into a single layer, suitable for counting (Kearns and Inouye, 1993).

We made a reference pollen collection of all flowering plants in the vicinity of our plots. We did not collect grass pollen, however, which may account for some of the pollen grains we were unable to identify. Prior to counting pollen on collected stigmas, counters familiarized themselves with the reference collection by hand drawing and measuring pollen from each collected species. Pollen on stigmas was identified and counted by visually scanning the entire slide, since squashing the stigma spread the pollen out away from it. When a pollen grain could not be identified using the reference collection or other resources available to us, it was given a unique ID that we used to classify other grains on other slides. Each of three counters kept their own list of unknowns, which we did not try to reconcile, so the number of unknown species is inflated. Stigmas from 653 flowers were evaluated for pollen loads. In all, we counted 175,507 pollen grains divided among 23 identified pollen species and 6192 pollen grains divided among 38 unknown pollen morphotypes; approximately 3% of pollen grains counted were of unknown species.

2.5. Statistical analysis

We used mixed models with type III sums of squares (PROC MIXED; SAS 8.02 (SAS Institute, 1999)) to identify differences in visitation rates to native plant species in plots in *Euphorbia*-infested sites and in sites >100 m from an infestation. Dependent variables were number of visits to flowers of native species, which were analyzed separately; independent variables included visitor taxon, infestation, year and all possible interactions. Plot was the random variable nested within infestation. A parallel analysis was conducted with genus within the Halictidae replacing visitor taxon as an independent variable for 2001 only. The abundance of flowering conspecifics and other plant species within and adjacent to the visitation plot were used as covariates to control for differences in flower abundance among plots; the number of individuals of other species was never statistically significant and was excluded from analyses presented in this paper.

We also used mixed models to determine the effect of infestation on (1) number of conspecific pollen grains, (2) number of leafy spurge pollen grains, (3) number of pollen species, and (4) proportion of heterospecific pollen on stigmas of each native species. Because we had two years of data for

Linum and *Oxytropis*, we ran one analysis with infestation, stigma species, year and all possible interactions as independent variables for these two species. A second analysis, for 2001 only, used all species sampled in that year, with infestation, stigma species and their interaction as independent variables. Total number of conspecific flowers within and adjacent to the plot was used as a covariate to separate effects of flower abundance from effects of infestation on conspecific pollen. All quantitative variables with the exception of proportion of heterospecific pollen were log transformed (after adding 1) to improve normality. Proportion of heterospecific pollen was square-root transformed prior to analysis, also to improve normality.

3. Results

Plots contained 1.1 ± 0.04 flowering species (mean \pm SE) in non-infested areas and 1.9 ± 0.03 (mean \pm SE) in infested areas ($F = 303.87$, $df = 1$, 427 , $p < 0.0001$); the higher number of species within infestations is attributable to the presence of *Euphorbia* in plots. Of 299 observations of insects moving between flowers within a plot, only 8 involved >1 species. The number of conspecific target flowers (other than leafy spurge) in a plot averaged 15.4 ± 0.86 in non-infested areas and 11.0 ± 0.65 in infested areas, a significant difference ($F = 16.41$, $df = 1$, 427 , $p < 0.0001$); total flowers in the plots (including *Euphorbia*) did not vary between non-infested and infested plots (15.4 ± 1.1 and 17.5 ± 0.8 , respectively, $F = 2.36$, $df = 1$, 427 , $p = .1252$). Plots in infested areas averaged 6.4 ± 7.0 leafy spurge stems.

3.1. Visitation

Native species in infested plots received 89% as many visits as in non-infested plots in 2000. In contrast, in 2001 native species in infested plots received only 57% as many total visits as did those in non-infested plots ($F = 3.93$, $df = 1$, 82 , $p = 0.05$ for the infestation by year interaction). Significantly more bees visited *Linum* in non-infested than infested sites in 2001, but not 2000 when visitation was similar between infestation levels (Fig. 1 and Table 1; least square means and standard errors for all visitation analyses are included in Appendix A). Bees and flies were the most common visitors to *Linum*. Like *Linum*, *Campanula* received more visits by bees in non-infested than in infested areas in 2001, but the reverse was true in 2000, when more visits were recorded in infested than in non-infested areas (Fig. 1). Flies were more common visitors to all native plant species in 2001 than in 2000. We recorded no visits by Lepidoptera or wasps to *Campanula*, and few by *Bombus*. Unlike *Linum* and *Campanula*, infestation by *Euphorbia* did not significantly influence visitation to *Oxytropis* (Fig. 1). The significant insect taxon by year interaction (Table 1) reflected strong shifts in visitation by *Bombus*, flies and Lepidoptera to *Oxytropis* between years. In contrast to the native species, we found no significant differences in visitation to *Euphorbia* itself between years (Table 1); flies were by far the most common visitors in both years (Fig. 1).

We also examined visitation by native bee taxa, other than *Bombus*, we could identify in the field, including the genera *Dialictus*, *Halictus*, *Agapostemon* and *Lasioglossum* in the family

Halictidae. This analysis was restricted to 2001, when we had more confidence in our identification of the bees. Halictids in the four genera above comprised 66% of our observations of bees in 2001, with the remainder made up of apids (*Apis mellifera*, the only exotic bee encountered, was recorded in only six plots), andrenids, megachilids and unidentified halictids (based on the sample identified in 2000; see Section 2); trends in the unknown bees collectively followed those of the halictids. Overall, we recorded nearly three times as many visits by halictids in non-infested sites as we did in infested sites (0.96 ± 0.08 and 0.33 ± 0.06 , ln-transformed least square mean \pm SE, respectively) in 2001. Visits to *Linum* varied with both bee taxon and infestation, but there was no interaction between the variables (Fig. 2 and Table 2). There were fewer visits by halictids of all taxa within infested sites than in non-infested sites. *Dialictus* and *Halictus* were the most common genera of bees to visit *Linum*. Visits by halictids to *Campanula* were also significantly reduced in sites infested by *Euphorbia*. *Dialictus* spp. tended to be the most common visitors to *Campanula*, but the differences among bee taxa were not statistically significant. *Oxytropis* had a non-significant trend toward higher visitation by halictids in non-infested sites, but there were no differences among taxa. *Euphorbia* itself was more commonly visited by *Dialictus* spp. than other bee taxa.

3.2. Pollen loads on stigmas

The amount of conspecific pollen on stigmas of *Linum* and *Oxytropis* was greater in the absence of *Euphorbia* than within an infestation (Table 3), and this did not vary between 2000 and 2001 (Table 4). Very little *Euphorbia* pollen was found on these two native species and this did not vary significantly with infestation or species. Suggestive of preferences of generalist pollinators for *Linum*, we found more pollen species and a larger proportion of heterospecific pollen on *Linum* than on *Oxytropis* stigmas (Table 3), and this was not influenced by infestation and did not vary between 2000 and 2001 (Table 4).

Looking only at 2001, but including all six species sampled that year, similar patterns emerge. The presence of *Euphorbia* within 100 m was significantly associated with fewer conspecific pollen grains on stigmas of native species (Fig. 3 and Table 5). The small amount of *Euphorbia* pollen we found on native stigmas was marginally greater in infested than in non-infested sites (Fig. 3 and Table 5). Two species, *Calylophus* and *Vicia*, had no *Euphorbia* pollen at all and could not be included in the analysis. The fact that we encountered *Euphorbia* pollen in non-infested sites implies that the pollen moved >100 m, at least in a few cases. Overall, 65 of the 653 flowers examined had *Euphorbia* pollen on at least one of their stigmas; 13 of these were collected in non-infested sites and 42 in infested sites. We found fewer pollen species on stigmas of native plants in infested than in non-infested sites but the proportion of heterospecific pollen on stigmas was greater for most species in infested than in non-infested sites (Fig. 3). *Linum* was an exception to this trend, with a larger proportion of heterospecific pollen in non-infested sites in 2001. *Campanula* and *Sphaeralcea* were most likely to have several pollen species on their stigmas while *Vicia* never and *Oxytropis* very rarely had pollen from other species on their stigmas.

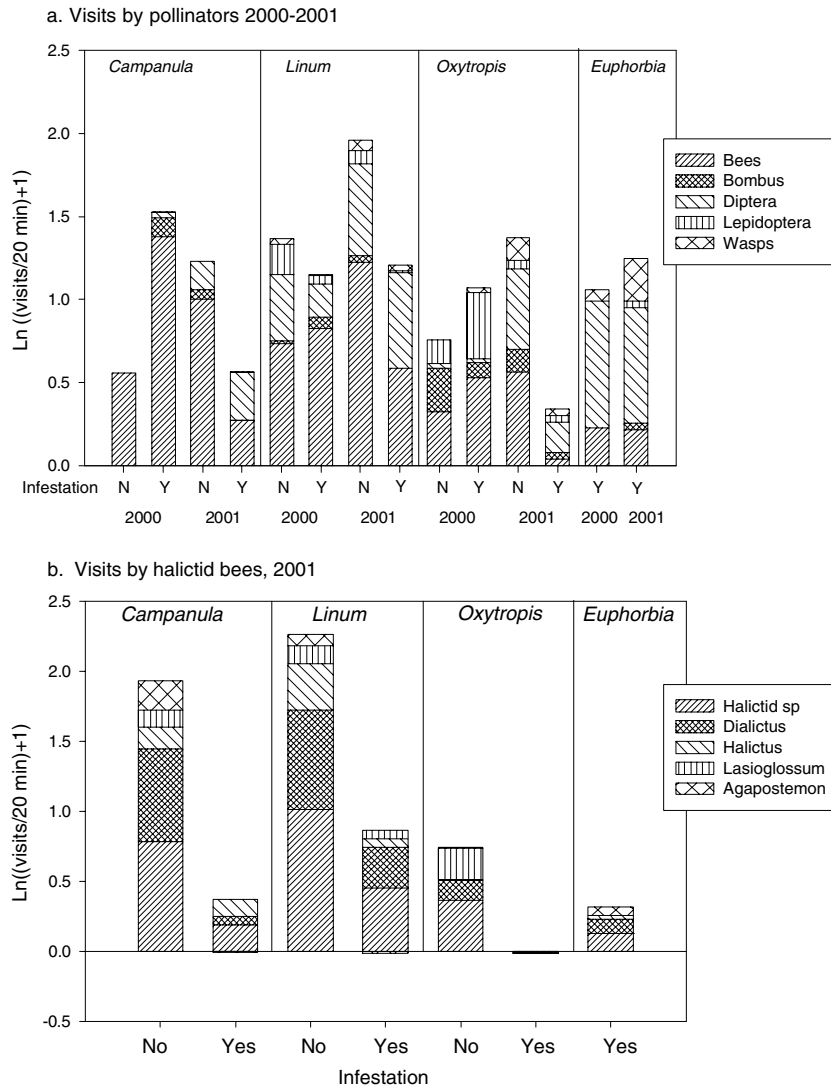


Fig. 1 – Cumulative visitation by pollinator taxa to native species and *Euphorbia*. (a) Visitation by all taxa in 2000–2001; (b) visitation by halictid bees in 2001.

4. Discussion

4.1. Visitation and conspecific pollen

The relationship between *Euphorbia* infestation and pollination of native plants at our study sites was not as straightforward as our hypotheses implied it would be. Although both visitation and deposition of conspecific pollen were lower on infested plots in most cases, this varied both by plant species and between the two years of the study. Year-to-year variation in pollination studies is to be expected: the variability inherent in pollination systems is well documented and many have warned of the difficulties in interpreting short-term studies (Fishbein and Venable, 1996; Herrera, 1988, 1995; Price et al., 2005; Roubik, 2001). Although we found clear effects of infestation on visitation by bees in 2001, results were more variable for 2000, when visits to *Campanula* were higher in infested than non-infested sites and visits to *Oxytropis* and *Linum* did not differ significantly with infestation.

Moragues and Traveset (2005) examined effects of the invasive *Carpobrotus* on several native species on an island in the Mediterranean and found similar variability in effects between years. Although, like Moragues and Traveset (2005), we found greater levels of visitation in infested plots for one species (*Campanula*) in one year, the lack of increased conspecific pollen on stigmas of *Campanula* suggests that we did not observe facilitation. Our results show that effects of infestation on insect visitation exist, but do not give an indication of how consistently they are expressed. Nonetheless, we never found significantly greater amounts of conspecific pollen on stigmas from infested areas and, in six of eight cases, the amount of conspecific pollen was significantly less on stigmas from infested areas.

Visitation and the amount of conspecific pollen on stigmas were not correlated in our study. Mean amount of conspecific pollen on *Linum* stigmas from non-infested plots did not vary between years even though overall visitation was much higher on non-infested plots in 2001 than 2000. Further, despite

Table 1 – ANOVA results for visitation by insects to *Linum lewisii*, *Campanula rotundifolia*, *Oxytropis lambertii* and *Euphorbia esula* in 2000–2001

Target species	Effect	Num. DF	Den. DF	F value	Pr > F
<i>L. lewisii</i>	Infestation	1	100	4.95	0.0283
	Insect taxa	4	404	56.72	<0.0001
	Year	1	404	1.92	0.1663
	Infestation × taxa	4	404	1.24	0.2938
	Infestation × year	1	404	1.62	0.2043
	Taxa × year	4	404	2.15	0.0741
	Infestation × taxa × year	4	404	3.75	0.0053
	Covariate	1	404	16.23	<0.0001
<i>C. rotundifolia</i>	Infestation	1	33	0.21	0.6522
	Insect taxa	4	131	24.84	<0.0001
	Year	1	131	0.19	0.6664
	Infestation × taxa	4	131	0.05	0.9947
	Infestation × year	1	131	6.21	0.0139
	Taxa × year	4	131	2.01	0.0962
	Infestation × taxa × year	4	131	6.18	0.0001
	Covariate	1	131	0	0.9594
<i>O. lambertii</i>	Infestation	1	42	0.8	0.3763
	Insect taxa	4	172	3.26	0.0132
	Year	1	172	0.01	0.9362
	Infestation × taxa	4	172	0.87	0.4808
	Infestation × year	1	172	3.3	0.0709
	Taxa × year	4	172	2.55	0.0411
	Infestation × taxa × year	4	172	1.22	0.3032
	Covariate	1	172	9.48	0.0024
<i>E. esula</i>	Year	1	348	0.95	0.3311
	Insect taxa	4	348	34.76	<0.0001
	Year × taxa	4	348	0.95	0.4353
	Covariate	1	348	16.3	<0.0001

The covariate is the number of flowers of the target species within the plot.

similar visitation rates between infested and non-infested plots in 2000 for both *Linum* and *Oxytropis*, conspecific pollen numbers were still lower on stigmas from infested plots. These observations imply that not only does the quantity of pollinators vary among years, but perhaps more importantly, so does the quality: more visitation does not always mean more conspecific pollen. Lau and Galloway (2004), studying the effects of low-efficiency, or “ugly”, pollinators on male function in *Campanula americana*, cautioned that increased visitation rates cannot be assumed to translate directly to increased fitness.

Having ruled out facilitation, does *Euphorbia* compete with native species for pollinators? Although lower levels of visitation and less conspecific pollen within infestations suggest competition, the observational nature of this study and our level of taxonomic resolution do not allow a definitive answer. However, the prevalence and consistency of Diptera in the pollinator assemblage of *Euphorbia*, compared with the prevalence of bees in that of the native species, suggests that, unlike the congeners *Lythrum salicaria* and *L. alatum* (Brown and Mitchell, 2001), these native plants may be experiencing relatively little competition for pollinator services with the invasive. Memmott and Waser (2002) demonstrated via food-web analyses that invasive plant species have become integrated into the interaction webs of the pollinator communities they studied. However, they

found that alien plants were mainly pollinated by generalists. Results of our study agree, in that flies were the primary visitors to *Euphorbia*. Although bees were observed to visit *Euphorbia*, the magnitude of this visitation did not, on average, balance the deficit seen in visitation to natives in infested sites.

Flies did make a substantial contribution to the pollinator community of one native species, *Linum*, and they have been shown to effectively pollinate this species in other locations (Kearns and Inouye, 1994). Flies were marginally less common visitors to *Linum* in infested than non-infested plots in 2000, leaving open the possibility that *Euphorbia* was attracting pollinators from *Linum* in this year. Note that in 2001, when flies visited all species relatively frequently, there was no effect of infestation on fly visits to *Linum*. Thus, effects of infestation likely depend on the population size of pollinators in a given year.

Visitation by pollinators is known to be strongly influenced by flower density (Kunin, 1997). We statistically accounted for differences in native flower density between infested and non-infested plots in this study, yet still found a significant effect of infestation on conspecific pollen deposition. The native species we targeted were common and pollen was still sufficiently abundant to fertilize all the ovules (but see Mitchell (1997)). However, the combined effects of low density and less conspecific pollen transported

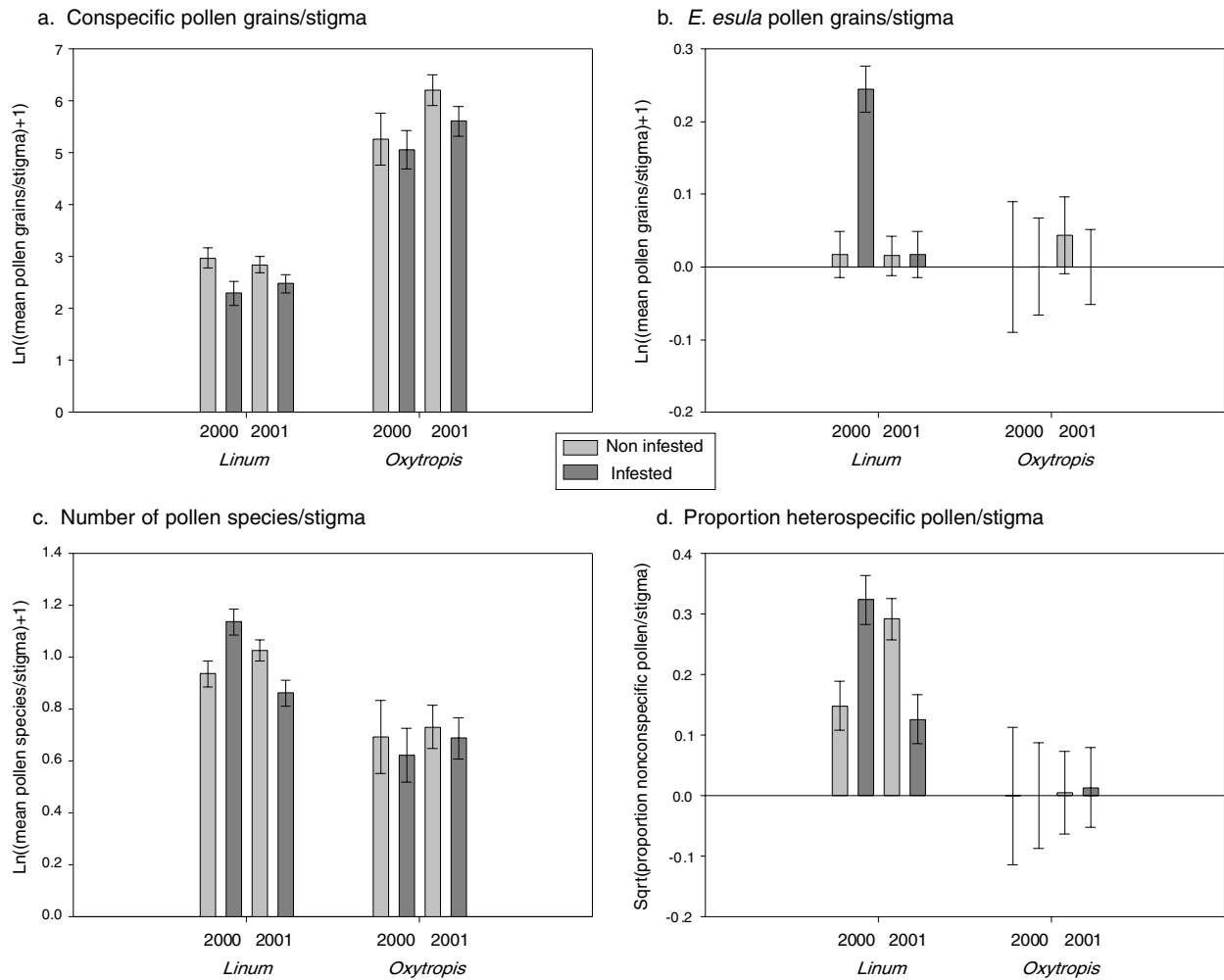


Fig. 2 – Pollen counts for stigmas collected from *Linum lewisii* and *Oxytropis lambertii* in 2000 and 2001. Shown are least square means of transformed ($\ln(n + 1)$) counts; proportions were square-root transformed. (a) Conspecific pollen; (b) *Euphorbia* pollen; (c) number of pollen species; (d) proportion of heterospecific pollen.

Table 2 – ANOVA results for visitation by halictid bees to *Linum lewisii*, *Campanula rotundifolia*, *Oxytropis lambertii* and *Euphorbia esula* in 2001

Target species	Effect	Num. DF	Den. DF	F value	Pr > F
<i>L. lewisii</i>	Infested	1	58	8.85	0.0043
	Insect taxa	4	231	19.5	<.0001
	Infested × taxa	4	231	2.47	0.0452
	Covariate	1	231	6.89	0.0092
<i>C. rotundifolia</i>	Infested	1	20	4.43	0.0481
	Insect taxa	4	84	3.95	0.0055
	Infested × taxa	4	84	2.12	0.0856
	Covariate	1	84	1.06	0.3052
<i>O. lambertii</i>	Infested	1	13	5.75	0.0322
	Insect taxa	4	56	1.96	0.1126
	Infested × taxa	4	56	1.96	0.1126
	Covariate	1	56	5.48	0.0228
<i>E. esula</i>	Insect taxa	4	236	2.66	0.0333
	Covariate	1	236	0.01	0.9292

The covariate is the number of flowers of the target species within the plot.

Table 3 – Effects of infestation and native species from which the stigma was collected (stigma species) on pollen deposition on native stigmas

Variable	Effect			
	Infestation	Stigma sp.	Mean ^a	Std. error
Conspecific pollen	No		4.3	0.16
	Yes		3.9	0.14
		<i>Linum</i>	2.6	0.095
		<i>Oxytropis</i>	5.5	0.19
Number of pollen species		<i>Linum</i>	0.99	0.024
		<i>Oxytropis</i>	0.68	0.052
Proportion of heterospecific pollen		<i>Linum</i>	0.22	0.020
		<i>Oxytropis</i>	0.0048	0.043

Least square means and their standard errors are shown for the highest order effect with a significant ($p \leq 0.05$) *F* value (see Table 4). Note that there were no significant effects of *Euphorbia* pollen on stigmas, so that variable is not included in this table.

^a Units for “Conspecific pollen” are $\ln(n+1)$ pollen grains/stigma; units for “Number of pollen species” are $\ln(n+1)$ *N* species; units for “Proportion heterospecific pollen” are $\sqrt{\text{proportion of total pollen on stigma that was not conspecific}}$.

Table 4 – ANOVA results for pollen counts on stigmas of *Linum lewisii* and *Oxytropis lambertii* (listed as “Stigma species”) in 2000 and 2001

Variable	Type 3 tests of fixed effects				
	Effect	Num. DF	Den. DF	<i>F</i>	<i>P</i>
Conspecific pollen	Infestation	1	101	4.85	0.0299
	Stigma sp.	1	305	187.19	<.0001
	Year	1	305	3.42	0.0652
	Infestation \times stigma sp.	1	305	0.09	0.7696
	Infestation \times year	1	305	0.01	0.9243
	Stigma sp. \times year	1	305	3.03	0.0825
	Infestation \times stigma sp. \times year	1	305	0.74	0.3919
	Covariate	1	305	0.69	0.407
Leafy spurge pollen	Infestation	1	342	1.59	0.2087
	Stigma sp.	1	342	2.86	0.0919
	Year	1	342	1.59	0.2086
	Infestation \times stigma sp.	1	342	3.41	0.0656
	Infestation \times year	1	342	3.33	0.0689
	Stigma sp. \times year	1	342	3.41	0.0658
	Infestation \times stigma sp. \times year	1	342	1.53	0.2169
Number of pollen species	Infestation	1	342	0.11	0.7382
	Stigma sp.	1	342	28.39	<.0001
	Year	1	342	0.13	0.7238
	Infestation \times stigma sp.	1	342	0.41	0.52
	Infestation \times year	1	342	2.17	0.1419
	Stigma sp. \times year	1	342	1.54	0.2155
	Infestation \times stigma sp. \times year	1	342	2.89	0.0899
Proportion heterospecific pollen	Infestation	1	332	0.01	0.9225
	Stigma sp.	1	332	21.17	<.0001
	Year	1	332	0.03	0.8542
	Infestation \times stigma sp.	1	332	0	0.9954
	Infestation \times year	1	332	3.09	0.0795
	Stigma sp. \times year	1	332	0.15	0.7006
	Infestation \times stigma sp. \times year	1	332	3.42	0.0652

The covariate is the number of flowers of the target species within and adjacent to the plot.

in infested areas would likely put rare species within *Euphorbia* infestations at risk of pollen limitation, at least in some years.

The observational nature of this study imposes some limitations on our interpretation, in addition to the assessment

of competition described above. There may have been qualities that varied systematically between infested and non-infested areas that were important to pollinators but that we did not measure, such as nest sites for ground-dwelling bees, or suitable woody vegetation for stem-nesters.

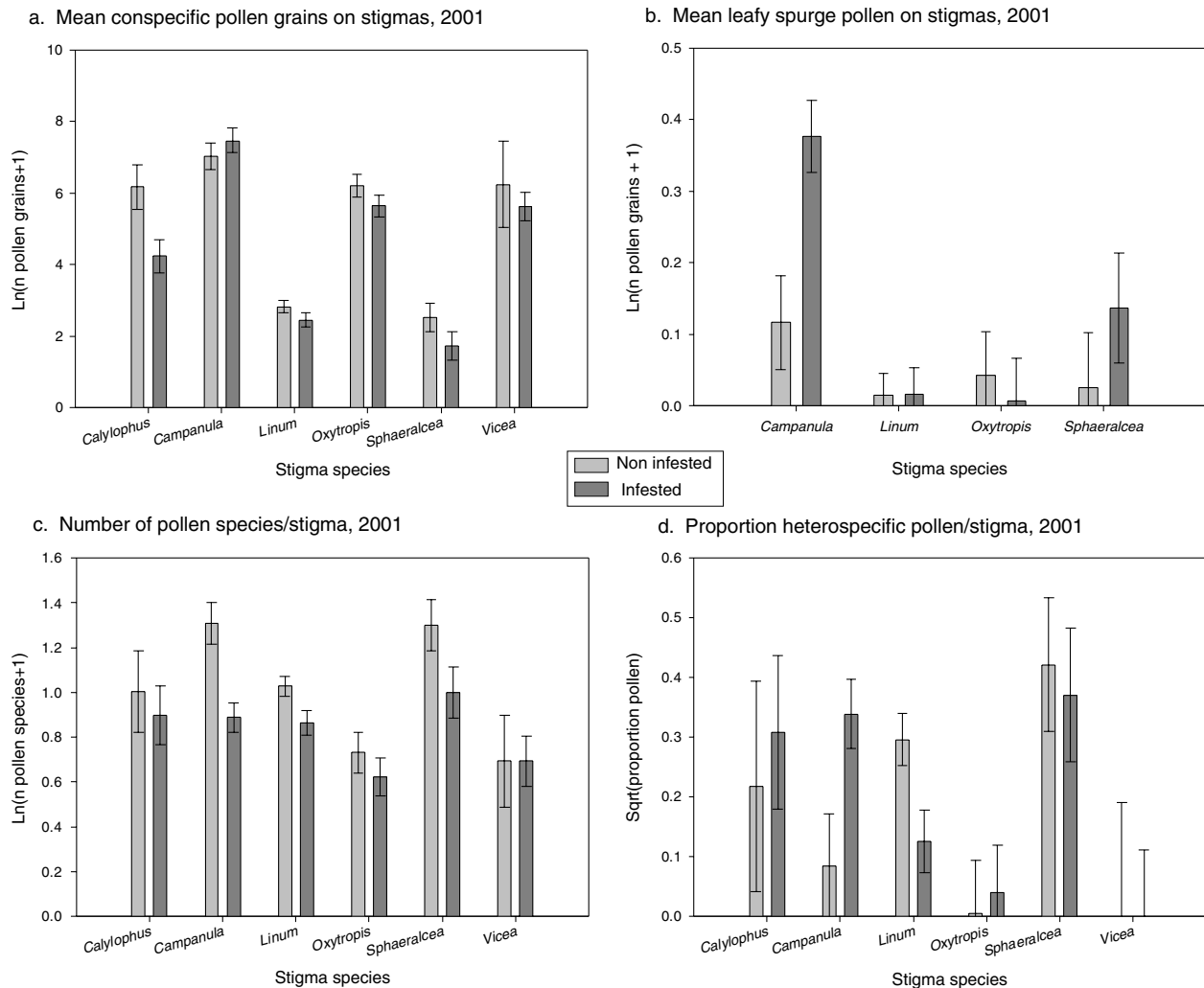


Fig. 3 – Pollen counts for stigmas collected from *Calylophus*, *Campanula*, *Linum*, *Oxytropis*, *Sphaeralcea* and *Vicia* in 2001. Shown are least square means of transformed ($\ln(n + 1)$) counts; proportions were square-root transformed. (a) Conspecific pollen; (b) *Euphorbia* pollen; (c) number of pollen species; (d) proportion of heterospecific pollen.

Table 5 – ANOVA results for counts of pollen on stigmas of *Calylophus serrulatus*, *Campanula rotundifolia*, *Linum lewisii*, *Oxytropis lambertii*, *Sphaeralcea coccinea* and *Vicia americana* in 2001

Response variable	Effect	Type 3 tests of fixed effects			
		Num. DF	Den. DF	F	P
Conspecific pollen	Infestation	1	92	4.78	0.0314
	Stigma sp.	5	275	81.88	<.0001
	Infestation × stigma sp.	5	275	1.48	0.1963
	Covariate	1	275	0.72	0.3961
Leafy spurge pollen	Infestation	1	257	3.99	0.0468
	Stigma sp.	3	257	8.14	<.0001
	Infestation × stigma sp.	3	257	2.94	0.0336
Number of pollen species	Infestation	1	291	7.37	0.007
	Stigma sp.	5	291	7.46	<.0001
	Infestation × stigma sp.	5	291	1.18	0.3171
Proportion heterospecific pollen	Infestation	1	280	0.17	0.684
	Stigma sp.	5	280	3.73	0.0027
	Infestation × stigma sp.	5	280	2.46	0.0332

4.2. Improper pollen transfer

In addition to influencing visitation rates and deposition of conspecific pollen, native plants within infestations may experience increased deposition of heterospecific pollen. Empirical studies have generally found little invasive pollen on native stigmas (Aigner, 2004; Moragues and Traveset, 2005) and our study is no exception. We found only very small amounts of *Euphorbia* pollen on native stigmas (no species had a back-transformed mean >0.5 grains/stigma), although the amounts varied significantly among native species; *Campanula* and *Linum* had greater amounts of *Euphorbia* pollen than other species in at least one year of the study. Zygomorphic species *Oxytropis* and *Vicia* were largely immune from *Euphorbia* pollen, as was actinomorphic species *Calylophus*: none was ever found on *Vicia* or *Calylophus* stigmas. Although pollinators may be more likely to act as generalists among morphologically similar species (Kunin, 1993, 1997), we found no evidence that species more similar to *Euphorbia*, in terms of flower shape (e.g., *Linum*, *Sphaeralcea*) or color (*Calylophus*) received more *Euphorbia* pollen than did dissimilar flowers (e.g., *Campanula*, *Oxytropis*, *Vicia*). Pollinators may discern patterns of flower similarities that differ from our broad categorizations of symmetry and visible color, however.

If *Euphorbia* infestations attract greater numbers of generalist pollinators, we would expect higher numbers of pollen species and greater proportions of heterospecific pollen on native species within these infestations. In general, we found fewer species of pollen on stigmas from infested sites and inconsistent differences in proportions of heterospecific pollen, suggesting that, if *Euphorbia* is attracting generalist pollinators, this does not translate into IPT for native species. Although contrary to our expectation, this result may reflect an indirect effect of leafy spurge infestation, in that species richness has been found to be lower within dense infestations (Belcher (1989); Larson, unpublished data). If fewer plant species exist within the foraging area of pollinators, fewer pollen species would be available for deposition on stigmas.

The variability we found in heterospecific pollen on stigmas once again emphasizes our limited ability to generalize about effects of infestation. Given the relatively low amounts of *Euphorbia* pollen and proportions of heterospecific pollen (ranging from a back-transformed mean of $<1\%$ for *Vicia* and *Oxytropis* to 14–18% for *Sphaeralcea*), the differences we found may have little biological significance for most species. However, we did find that introduction of *Euphorbia* pollen onto hand pollinated *Linum* flowers resulted in significantly lower seed set than that found for flowers on the same plant that were only hand pollinated (least square means = 5 ± 0.84 and 9 ± 0.64 for spurge introduced vs. no spurge on fully pollinated flowers, $F = 7.34$, $df = 2, 8$, $p = 0.0155$; Larson, unpublished data), leaving open the possibility that small quantities of *Euphorbia* pollen may have fitness effects.

Chittka and Schürkens (2001) proposed that competition between native and invasive plants may occur at substantially greater distances than previously thought, due to the distances traveled by pollinators. Our results support that

proposition. Approximately 10% of the flowers we sampled had *Euphorbia* pollen. The amount of *Euphorbia* pollen on stigmas varied only slightly between infested and non-infested sites, thus indicating that the invasive pollen is transported, at least occasionally, >100 m, while interspecific competition for light and nutrients typically occurs within a few cm of the plant.

4.3. Management implications

The primary effects of *Euphorbia* infestation on pollination of native plants were a decline in conspecific pollen deposited on stigmas in both years and in visitation by bees, especially *Halictus* spp. and *Dialictus* spp. in the family Halictidae, in one of the two years studied. Given that we detected declines in conspecific pollen in species that are relatively common, the potential for significant pollen shortfalls in rare species is high. Managers need to be aware of the danger of pollen limitation, especially in rare or uncommon plant species. Clonal or long-lived species may persist for considerable periods of time in the absence of effective pollination, leading to what Johnson and Steiner (2000) have called “an insidious form of delayed extinction”. Most land managers are aware of the locations of species of concern on their properties. We would encourage them to monitor seed set (which is considerably easier to accomplish than are studies of pollination) of the insect-pollinated species if significant encroachment of invasive species is noted. If reductions in seed set are noted, this should trigger more extensive studies of potential mechanisms, including pollen limitation and IPT.

Of equal importance is the observation that native halictid bees are less frequent visitors in infested areas in some years. Despite a general increase in visits by halictids in non-infested areas between 2000 and 2001, visits in infested areas were down substantially over the same time period. Our results add to recent concern over the general decline in pollinators (Kearns et al., 1998) and accentuate the need to understand the role that invasive species play at all levels of the ecosystems they invade. Because halictids are notoriously difficult to identify, they present a special challenge to land managers who wish to monitor their populations. Additional research to determine the reasons for fewer halictids within *Euphorbia* infestations might suggest indirect methods of assessing risk to halictid populations that would be more accessible to land managers than direct monitoring of the bee populations.

Finally, the variability we observed between years requires further investigation. We found no obvious correlations with local differences in temperature or precipitation between the two years, so we cannot say what might have caused the variability we observed. Managers will need to know how frequently to expect effects of infestation to occur and to know if concurrency with other environmental fluctuations might exacerbate effects of infestation.

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Appendix A

Visitation by insects to *Linum lewisii*, *Campanula rotundifolia*, *Oxytropis lambertii* and *Euphorbia esula*. Part a includes all insect visitor taxa across the two years of the study. Note that "Bees" exclude bumblebees, which are listed as "*Bombus*". Part b includes only those bees in the family Halictidae in 2001. Least square means ($\ln(n+1)$ pollen grains/stigma) and their standard errors are shown for the highest order effect with a significant ($p \leq 0.05$) F value.

Target species	Infested	Insect taxa	Year	Visits/20 min	Std. error
Part a					
<i>L. lewisii</i>	no	Bees	2000	0.74	0.10
	yes	Bees	2000	0.83	0.11
	no	Bees	2001	1.22	0.08
	yes	Bees	2001	0.59	0.09
	no	<i>Bombus</i>	2000	0.02	0.10
	yes	<i>Bombus</i>	2000	0.07	0.11
	no	<i>Bombus</i>	2001	0.04	0.08
	yes	<i>Bombus</i>	2001	-0.03	0.09
	no	Diptera	2000	0.40	0.10
	yes	Diptera	2000	0.20	0.11
	no	Diptera	2001	0.55	0.08
	yes	Diptera	2001	0.58	0.09
	no	Lepidoptera	2000	0.18	0.10
	yes	Lepidoptera	2000	0.05	0.11
	no	Lepidoptera	2001	0.08	0.08
	yes	Lepidoptera	2001	0.01	0.09
	no	Wasps	2000	0.03	0.10
	yes	Wasps	2000	0.00	0.11
	no	Wasps	2001	0.06	0.08
	yes	Wasps	2001	0.03	0.09
<i>C. rotundifolia</i>	no	Bees	2000	0.56	0.20
	yes	Bees	2000	1.38	0.12
	no	Bees	2001	1.00	0.11
	yes	Bees	2001	0.27	0.12
	no	<i>Bombus</i>	2000	0.00	0.20
	yes	<i>Bombus</i>	2000	0.11	0.12
	no	<i>Bombus</i>	2001	0.06	0.11
	yes	<i>Bombus</i>	2001	0.00	0.12
	no	Diptera	2000	0.00	0.20
	yes	Diptera	2000	0.04	0.12

Target species	Infested	Insect taxa	Year	Visits/20 min	Std. error
	no	Diptera	2001	0.17	0.11
	yes	Diptera	2001	0.29	0.12
	no	Lepidoptera	2000	0.00	0.20
	yes	Lepidoptera	2000	0.00	0.12
	no	Lepidoptera	2001	0.00	0.11
	yes	Lepidoptera	2001	0.00	0.12
	no	Wasps	2000	0.00	0.20
	yes	Wasps	2000	0.00	0.12
	no	Wasps	2001	0.00	0.11
	yes	Wasps	2001	0.00	0.12
<i>O. lambertii</i>	no	Bees	2000	0.43	0.08
	yes	Bees	2001	0.30	0.11
	no	<i>Bombus</i>	2000	0.18	0.08
	yes	<i>Bombus</i>	2001	0.09	0.11
	no	Diptera	2000	0.03	0.08
	yes	Diptera	2001	0.33	0.11
	no	Lepidoptera	2000	0.27	0.08
	yes	Lepidoptera	2001	0.05	0.11
	no	Wasps	2000	-0.01	0.08
	yes	Wasps	2001	0.09	0.11
<i>E. esula</i>	yes	Bees		0.22	0.05
	yes	<i>Bombus</i>		0.00	0.05
	yes	Diptera		0.73	0.05
	yes	Lepidoptera		0.01	0.05
	yes	Wasps		0.16	0.05
Target species	Infested	Insect taxa	Year	Visits/20 min	Std. error
Part b					
<i>L. lewisii</i>	No	<i>Agapostemon</i>	0.08	0.10	
	Yes	<i>Agapostemon</i>	-0.01	0.11	
	No	<i>Dialictus</i>	0.71	0.10	
	Yes	<i>Dialictus</i>	0.29	0.11	
	No	Halictid sp.	1.01	0.10	
	Yes	Halictid sp.	0.45	0.11	
	No	Halictus	0.33	0.10	
	Yes	Halictus	0.06	0.11	
	No	<i>Lasioglossum</i>	0.13	0.10	
	Yes	<i>Lasioglossum</i>	0.06	0.11	
<i>C. rotundifolia</i>	No		0.39	0.10	
	Yes		0.07	0.11	
		<i>Agapostemon</i>	0.10	0.11	
		<i>Dialictus</i>	0.36	0.11	
		Halictid sp.	0.48	0.11	
		Halictus	0.14	0.11	
		<i>Lasioglossum</i>	0.06	0.11	
<i>O. lambertii</i>	No		0.15	0.04	
	Yes		0.00	0.04	
<i>E. esula</i>	Yes	<i>Agapostemon</i>	0.07	0.04	
	Yes	<i>Dialictus</i>	0.10	0.04	
	Yes	Halictid sp.	0.13	0.04	
	Yes	Halictus	0.02	0.04	
	Yes	<i>Lasioglossum</i>	0.00	0.04	

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